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The community of medium-sized carnivores:

the interactions between species, habitats and rabies.

Katja Holmala

ACADEMIC DISSERTATION

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”Tiedon puussa asuu kyy.

Joka sitä lähestyy,

ikuisesti onneton

epäilyksen uhri on.

Autuas ken omin päin

elää, kuolee lailla täin!”

Lauri Viita, Tiedonpuu

Contents

List of original publications

This thesis is based on the following articles, which are referred to in the text by their roman numerals:

I Holmala, K. & Kauhala, K. 2006: Ecology of wildlife rabies in Europe. – Mammal Review, 36 (1), 17-36.

II Kauhala, K., Holmala, K., Lamners, W. & Schregel, J. 2006: Home ranges and densities of medium-sized carnivores in Southeast Finland with special reference to rabies spread. – Acta Theriologica, 51 (1), 1-13.

III Kauhala, K. & Holmala, K. 2006: Contact rate and risk of rabies spread between medium-sized carnivores in southeast Finland. – Annales Zoologici Fennici, 43, 348-357.

IV Holmala, K. & Kauhala, K. 2009: Habitat use of medium-sized carnivores in southeast Finland – Key habitats for rabies spread? – Annales Zoologici Fennici, 46, in press.

Contributions

The following table shows the major contributions of authors to the original articles.

	I	II	III	IV
Original idea	KK, KH	KK, KH	KK, KH	KH, KK
Data gathering	KH, KK	KH, WL, JS	KH, WL, JS	KH, WL, JS
Data analysis	KH, KK	KK, KH, WL	KK, KH	KH
Manuscript preparation	KH, KK	KK, KH, JS	KK, KH	KH, KK

KH Katja Holmala, KK Kaarina Kauhala, JS Julia Schregel, WL Wiebke Lammers

Abstract

The composition of the carnivore community influences the different forms of inter-specific interactions. Furthermore, inter-specific interactions of sympatric carnivores have important implications for intra-guild competition, epidemiology and strategies of species-specific population management.

Zoonooses, such as rabies, are diseases that can be transmitted from wildlife to people. Knowing the ecological characteristics of the species helps us to choose the right preventive actions and to time them accurately.

In this thesis, I have studied how raccoon dogs *Nyctereutes procyonoides*, European badgers *Meles meles*, red foxes *Vulpes vulpes* and domestic cats *Felis silvestris catus* act as species and as members of carnivore community, and how these interactions relate to the transmission risk of rabies.

In the study area, these species form a community of medium-sized and rather generalist predators. They live in the same areas, in spatially and temporally overlapping home ranges and use the same habitats and dens and even have similar diets. However, there is no direct evidence of competition. Shared dens point to good tolerance of other species. Numerous observations of animals moving in each other's proximity give similar clues. However, overlapping home ranges and similar habitat preferences lead to frequent inter-specific contacts, which increase the risk of possible rabies transmission.

The new insight of habitat use gained by this study illustrates the similar favouring of deciduous forests and fields by these medium-sized carnivores, creating a basis for contact zones, i.e. risky habitats for rabies transmission and spread. In case of an epizootic, targeting the control measures to the most used habitats could result in more rapid eradication of the disease. Further research is still needed to define the risky habitats for foxes.

These results have significant implications for the planning of rabies control. In order to reach viable management decisions, not only one or two species should be taken into consideration, but the whole community. In particular, this changes the perspective to animal densities, densities of individuals susceptible to diseases and the magnitude of preventive actions. Rabies should be considered as a multi-vector disease, at least in Finland and the Baltic states. Furthermore, all the topics addressed in this thesis are essential components for building an explicit rabies model for Finland. It is of interest for disease management to be able to model an epizootic with local parameters to reflect the real situation and also to suite best the local management needs. My results lead me to suggest that new models should be further developed with both foxes and raccoon dogs and even badgers as important vector species.

1 Introduction

Inter-specific interactions of sympatric carnivores have important implications for intra-guild competition, epidemiology and strategies for species-specific population management (Macdonald *et al.* 2004). Especially in rural areas, wildlife, cattle and pets come into frequent contact with each other. Also wildlife species, here medium-sized carnivores, interact. Moreover, the composition of the carnivore community influences the different forms of inter-specific interactions and, thereby, the probability of the between and within-species transmission of a disease with several hosts (Caley & Hone 2004). Therefore, it is important to understand the interactions in the whole community of carnivores instead of the ecology of just one species.

Zoonooses are diseases and infections that are naturally transmitted from wildlife to human. Some of these diseases are fatal to victims and even have economical significance. A large amount of money is spent yearly on managing diseases such as rabies (e.g. Aubert 1999) and bovine tuberculosis in Europe. Especially sylvatic (wildlife) rabies cases have been increasing in some countries in Eastern and Southern Europe during the last decade (Pötzsch *et al.* 2002).

Knowing the ecological characteristics of all vector (transmitter of a disease) species in the community helps to choose the right preventive actions and to time them accurately. Andral and colleagues (1982) discovered that a diseased fox *Vulpes vulpes* will behave very much like a healthy one. Therefore, in the absence of the disease the knowledge of the contacts between healthy animals can also help in estimating the effects of potential epizootic in different host densities and environmental conditions (habitats). Modelling of rabies epizootics can help to plan the preventive actions more efficiently. To further develop the models requires knowledge of local ecological parameters such as home range size, population density, habitat selection and contacts between individuals.

1.1. Interactions in the carnivore community

Species live in a community. The realized niche and the composition of the carnivore guild influence the different forms of inter-specific interactions. Similar-sized carnivores use similar resources, for example similar-sized prey, which may lead to competition (Rosenzweig 1966). Keddy (1989) defined competition as "the negative effects, which one organism has upon another by consuming, or controlling access to, a resource that is limited in availability." Competition may result in reduced densities of subordinate species (e.g. Linnell & Strand 2000). However, direct evidence of competition is very difficult to collect and therefore scarce.

Competition influences the interactions and behaviour of the species in question. For example the relations among predatory species in the North American

boreal forests are characterized by behavioural avoidance and intra-guild predation among many species (Polis *et al.* 1989). Resource overlap is commonly used to assess the potential for competition (Schoener 1983). The most intensive inter-specific competition on natural populations is documented between closely related species with similar ecological niche (Connell 1983, Schoener 1983). Raccoon dogs *Nyctereutes procyonoides*, badgers *Meles meles* and red foxes share many resources, which suggest that competition may occur among them.

Overlapping diets could possibly lead to some level of exploitative competition, if all carnivores foraged at the same time. Badgers, raccoon dogs and foxes are mainly crepuscular and can occupy similar ecological niches across a wide range of habitats and may compete over foods (e.g. earthworms *Lumbricus terrestris*, small vertebrates, eggs, fruit) as well as over suitable den sites (Table 1). In northern Belarus, there was little evidence of resource competition between foxes and raccoon dogs during the warm season regardless of their considerably overlapping diets (Sidorovich *et al.* 2000). However, raccoon dogs seemed to compete for food with foxes in the coldest season. In Finland, the food niches of raccoon dogs and badgers overlapped more with each other than with that of the foxes (Kauhala *et al.* 1998). However, their diets differed to some extent, which may help to avoid competition. The fox was the most carnivorous, the raccoon dog the most omnivorous while the badger concentrated on a more vegetable diet (Kauhala *et al.* 1998). Most agonistic encounters between carnivore species in seasonal environments occur when food is scarce (Palomares & Caro 1999). However, raccoon dogs and badgers are dormant when the food is scarcest in Finland. This might partly explain the coexistence of these species in boreal forests. Thus, niche segregation serves to reduce exploitative competition and facilitate the coexistence of similar species.

High diet overlap is estimated to further increase encounters of sympatric species, because in search of similar prey, they are likely to occupy similar habitats (Polis *et al.* 1989, Buskirk 1999). The possibility of encounters might be further heightened due to the fact that raccoon dogs and badgers, and badgers and foxes are known to share dens (Kowalczyk *et al.* 2000, Kauhala & Holmala 2006, Kowalczyk *et al.* 2008).

Documented records of raccoon dog–fox, raccoon dog–badger or badger-fox encounters are rather scarce. Even less is known about encounters of these species with domestic cats *Felis silvestris catus*. In a study of fox-badger encounters in England (Macdonald *et al.* 2004), badgers usually dominated in meetings with foxes. Nevertheless, most encounters were not aggressive, with each species apparently ignoring the other, yet remaining in their company. In Spain, foxes and badgers evidently coexisted peacefully, which might be facilitated in some areas by the use of rather different habitats during activity (Fedriani 1993, sited in Fedriani *et al.* 1999). It is more common that one species behaves as dominant over the other when they meet. However, if the

costs of direct aggression are too high and the benefits too low, avoiding a fight may be a preferable option (Huntingford & Turner 1987). Smaller body size, supplemented diet and different habitat selection excludes the domestic cat as a competitor for the above mentioned species. However, domestic cats are a noteworthy part of the carnivore community and also an important link for the transmission of zoonootic diseases to humans.

Table 1. *The main characteristics of the studied species.*

	Red fox	Raccoon dog	Badger	Cat
Size	3 – 14 kg, study animals 4- 6 kg [1]	4.5 – 9 kg, study animals 4 - 5 kg [1]	Large variation, study animals 5 - 7 kg	Large variation, study animals 3 - 4 kg
Diet	Carnivore, large variation in prey species [2]	Opportunistic omnivore [2]	Opportunistic omnivore, generalist [1]	Carnivore, largely provided by man [1]
Social system	Varies from solitary to groups, probably pairs in Finland, usually monogamous [3]	Pairs, monogamous [3]	Varies from solitary to groups, social system in Finland unclear [2]	Varies from solitary to groups (feral), in study area unclear [2]
Special features	Active year round	Hibernates part of winter [4]	Dormant in winter [3]	A pet
Dens	No permanent dens, day rests and pup dens [4]	Several dens used annually [5]	From a communal den to several temporary dens [4]	No dens
Home range	Territorial, rather stable, itinerant individuals, large variation [5]	South-central Finland: mean 9.5 km2, rather stable [6]	In some areas territorial, slight shift between seasons [5]	Large variation, Southern Sweden (MCP) 3.0-9.9 km2 [3]
Breeding season	From January to February, in northern areas also in March [6]	From February to March [7]	*Post-partum* in spring, another smaller peak in autumn [6]	Females in oestrus from January to October, males active year round [4]
References	1 Nowak 1991 2 Kauhala *et al.* 1998, Sidorovich *et al.* 2000 3 Voigt & Macdonald 1984, Cavallini 1996 4 Kowalczyk *et al.* 2000, Kauhala *et al.* 2006 5 Cavallini 1996, Baker & Harris 2004 6 Larivière & Pasitschniak-Arts 1996	1 Kauhala 1992 2 Kauhala *et al.* 1998, Sidorovich *et al.* 2000 3 Ward & Wurster-Hill 1990, Kauhala & Helle 1994 4 Ward & Wurster-Hill 1990, Kauhala *et al.* 2007 5 Kauhala *et al* 2006 6 Kauhala *et al.* 1993 7 Helle & Kauhala 1995	1Kauhala *et al.* 1998 2 Kruuk & Parish 1982 3 Bevanger & Lindström 1995 4 Kruuk & Parish 1982 5 Kruuk & Parish 1982 6 Creswell *et al.* 1992	1 Liberg 1984 2 own observation 3 Liberg & Sandell 1988 4 Germain *et al.* 2008

1.2. Rabies in wildlife

The rabies virus is a multi-host pathogen capable of infecting a wide range of species. It can infect all species of mammals, although some are more susceptible than others (Macdonald 1995). Mammalian reservoirs include the *Carnivora* and *Chiroptera*, but rabid dogs pose the greatest hazard worldwide (Rupprecht *et al.* 2002). Today, many countries in Europe are rabies-free (WHO 2007). Where terrestrial rabies still exists in Europe, it is mainly sylvatic rabies. Dog-mediated rabies has almost completely been eradicated, except from Turkey and Russia (Müller 2000). Although most cases elsewhere in Europe are in red foxes, the proportion of raccoon dog cases increases towards northeast and has grown during recent years; in 1999, 8 % of the reported wildlife rabies cases (n = 4269) were in raccoon dogs and 85% in foxes, the corresponding figures for 2006 (n = 13 652) being 14% and 81% (WHO 1999, 2006). Other wildlife (especially mustelids) has been infected, too. Humans in Europe are at most risk of rabies transmission from infected domestic animals, mainly from domestic cats (Pastoret *et al.* 1995).

Until recently, the epizootiology of rabies has been relatively simple in Europe, where the red fox has been the main wildlife rabies vector (e.g. Anderson *et al.* 1981, Pastoret *et al.* 1995, review in Holmala & Kauhala 2006), and numerous authors (e.g. Blancou 1988, Macdonald & Voigt 1985) have described fox rabies enzootics in Europe. Many of the features of rabies outbreaks can be explained in terms of fox behaviour, as can some of the differences between outbreaks in different areas (Macdonald & Voigt 1985). It was even thought that rabies epizootic could not be maintained by other wild species (Lloyd 1977). However, nowadays the raccoon dog appears to be the second most important wildlife species infected with rabies (Westerling 1991, Pötzsch *et al.* 2002, Holmala & Kauhala 2006). With this introduced canid, the epizootiological situation in Europe has been altered. The situation with several vector species adds to the complexity of the epidemiology of rabies (Macdonald 1980, Kaplan 1985, Blancou 1988).

1.3. Transmission of rabies and carnivore guild

Transmissions, surveillance, and control of vector-borne diseases depend on the ecology of vectors, on the environmental determinants of vector distribution, and in the case of vector-borne zoonooses, also the ecology of reservoir hosts. In Europe, red fox and raccoon dog are the two main vector species to be considered. Cross-species transmission (spillover) typically results in short-lived chains of transmission as in badgers (Wandeler *et al.* 1994). Badgers are fairly susceptible to the rabies infection

and they can transmit the virus easily, but might not alone be able to sustain an epizootic (Wandeler *et al.* 1974, Smith 2002, Smith & Wilkinson 2002). Occasionally, cross-species transmission may lead to sustained transmission when a virus is transmitted over a species barrier to a new host species with favourable ecological, genetic and behavioural characteristics (e.g. from dog to red fox; Anderson *et al.* 1981, Bourhy *et al.* 1999).

The composition of the carnivore community influences the probability of the transmission of a disease and the actual transmission event, since it influences both the densities of susceptible animals and the number of interacting (vector) species. Rabies persists when there are sufficient individuals to sustain intra-specific transmission, i.e. if an infected individual transmits the virus during the short period of virus excretion to an adequate number of susceptible individuals (Wandeler *et al.* 1988, Childs *et al.* 2007). This is, according to Kendal's Threshold Theorem, more than one susceptible individual infected by each infective individual (Baily 1975). Consequently, rabies transmission ceases when an infected individual transmits the disease approximately to less than one individual (Ginsberg & Macdonald 1990).

Directly transmitted diseases of short duration, long incubation periods and high case-mortality require high host densities in order to persist (Carey & McLean 1983). Fox density between 0.25–1.0 fox/km^2 is the commonly reported range for threshold densities of a rabies epizootic (Toma & Andral 1977, Anderson *et al.* 1981, David *et al.* 1982). In poorer environmental conditions, even much lower densities of predators have been able to sustain epizootics (Thyul'ko *et al.* 2002). Likewise, lower densities would be enough for an epizootic to form also in cases involving two vector species (Singer *et al.* 2008). During the 1980´s epizootic in Finland, a density of 0.45-1.3 animals/km^2 in mixed fox-raccoon dog populations was estimated (Nyberg *et al.* 1992). In addition, there has been a rise in the fox populations in certain areas of Western Europe due to successful European vaccination campaigns (Chautan *et al.* 2000).

Inter- and intra-species interactions also affect the scale and the speed of an epizootic. Rabies is usually transmitted through bites or, very rarely, aerosol contamination (Rupprecht *et al.* 2002). Spatial spread of rabies occurs either within territory, through neighbour-to-neighbour infection or through inter-territorial movements (temporary and permanent dispersal) of infected animals. For example, in areas of high fox density, the non-dispersing animals probably determine the rate of rabies spread (Saunders *et al.* 1997), indicating transmission either within territory or through neighbour-to-neighbour infection. The front of rabies epizootic may sometimes jump forward even 100 km. For example, the epizootic in Finland in 1989 started about 70 km southeast from the Finnish-Russian border (Westerling 1991). These leaps are probably due to dispersing rabid individuals (Macdonald & Bacon 1982).

Where sympatric wildlife species are infected with disease, quantifying intra- and inter-specific transmission rates enables the host status of different species to be determined (Caley & Hone 2004). Transmission rate estimates are usually based on the contact rates estimated in the field. The term contact rate refers to the number of different animals each individual might contact during a defined time period. The greatest contact rate should be during the mating season (Pastoret & Brochier 1999). For foxes this is usually from January to February (Larivière & Pasitschniak-Arts 1996), in northern areas also in March, for badgers post-partum in spring, although another smaller peak occurs in autumn (Creswell *et al.* 1992) and for raccoon dogs from February to March (Ward & Wurster-Hill 1990, Helle & Kauhala 1995). Both foxes and badgers are territorial at moderate to high densities, and inter-territorial contacts are likely to occur on a regular basis (Madconald 1980).

When controlled experiments of disease transmission are impossible (as in the case of rabies), the rates of inter- and intra-specific transmission may alternatively be estimated by mathematical modelling (Caley & Hone 2004). For example, Rhodes and colleagues (1998) demonstrated that rabies would not occur in side-striped jackals *Canis adustus* in Zimbabwe without significant inter-specific transmission from domestic dogs. In another model, the rabies epidemic could be established in a community of foxes and raccoon dogs in Finland below the threshold densities assumed for rabies and one vector species (Singer *et al.* 2008). In some epidemiological models, the risk of disease in a spillover species (cat) has been linked to the temporal dynamics of the disease in a wildlife reservoir (raccoon *Procyon lotor*) (Gordon *et al.* 2004). Other models have further emphasised the great sensitivity of rabies epizootiology to contact rate (Bacon & Macdonald 1980, Anderson *et al.* 1981, Macdonald & Voigt 1985).

Disease modelling helps to plan the preventive actions, e.g. bait vaccinations that are more cost-efficient and lead to successful epizootic management. For the modelling of an epizootic, information is needed on ecological parameters, such as home range size, animal density, dispersal distances, as well as several demographic features of the populations (mortality, age structure, etc.), intra- and inter-specific contact rates and habitat use (Macdonald & Voigt 1985). The home range size is negatively correlated with the population density and positively correlated with the dispersal distance (Trewhella *et al.* 1988). High density of susceptible animals increases the risk of rabies epizootic. For example, for both red and arctic fox, rabies epizootics coincide with the relatively high fox densities (Macdonald 1980). This correlation to vector population density is also found in other epizootic diseases. Long dispersal distances are linked to the speed of the spread of rabies (Macdonald & Bacon 1982). Overlapping home ranges and similar habitat use affect the likelihood of intra- and inter-species contacts. It is important that models simulate the potential spread of rabies in wildlife as realistically as possible by including data

of the local circumstances and the ecology of the potential vector species.

1.4. Habitat use and rabies management

The spatial distribution of vector-borne diseases is restricted typically by the geographical range of the vector or reservoir host(s) and by their habitat preferences (Kitron 1998). Home range size and shape are the results of habitat selection by an animal searching for a suitable area containing all the necessary resources for survival and reproduction (second order selection, Johnson 1980). Therefore, individuals should forage in those habitats where the return of fitness is maximized. Consequently, knowing the density response of a species at different habitat scales allows us to evaluate the significance of the habitat to the patterns of coexistence of interacting species (Schoener 1974) and diseases.

Species that select some patches over others probably do so because the patches differ in the density of resources (Rosenzweig 1974). The resource dispersion hypothesis predicts that spatial organization will be determined by the dispersion of resource patches (RDH; Macdonald 1983). The attempts to explain the spatial and social organization of badgers have centred on food dispersion (e.g. Kruuk & Parish 1982, Macdonald 1983, Woodroffe & Macdonald 1993). In fact, the home range sizes of badgers and foxes correlate with the dispersion of important food patches (Macdonald 1981, Brȼseth *et al.* 1997). The same correlation has been noted also between the raccoon dogs´ home range sizes and the dispersion of the most favoured habitat patches (Holmala & Kauhala, unpubl.). An alternative theory predicts that available den sites may determine the size and shape of the home ranges for badgers and foxes (Doncaster & Woodroffe 1993, Roper 1993).

There is evidence that habitat-linked landscape effects (habitat quality and habitat pattern) are important in maintaining persistent (rabies) virus-host associations (Carey & McLean 1983). Local differences in the amount of animals, e.g. foxes, at least partly reflect the variation on resource availability (Macdonald & Voigt 1985) and mortality. It is common knowledge, reinforced by several published studies that fox density varies among habitats. For example, on a worldwide basis, red foxes are most abundant in areas with heterogeneous habitats (Lloyd 1980). Moreover, the habitat features have even been used to estimate fox densities (Macdonald *et al.* 1981). Also, both the frequency of encounters between foxes and the contact rate of rabies vary between habitats (Macdonald & Bacon 1982). Other studies have indicated that habitat types have influenced the spread (speed and intensity) of rabies (e.g. Steck & Wandeler 1980, Pool & Hacker 1982, Carey & McLean 1983, Sanson & Pearson 1997 in Gylys *et al.* 1998). Therefore, the study of habitat selection and use of a disease vector species also provides an important tool for rabies risk analysis and management.

To be able to efficiently control wildlife diseases, the composition of the carnivore guild and the intra- and inter-

species interactions must be known. Andral and colleagues (1982) found that a diseased fox will behave very much like a healthy one. However, sometimes rabid foxes may spend more time near the boundaries of they home ranges (Artois *et al.* 1991) making the contacts even more likely. During the Finnish epizootic in 1988-1989, both rabid foxes and raccoon dogs seemed to remain in their original home ranges, although in the raccoon dog population, signs of social uneasiness were observed (Westerling 1991). Therefore, knowing how healthy animals contact other individuals, it is possible to try to estimate the contact rate between rabid and healthy animals.

The knowledge of the ecological characteristics of the species helps us to choose the right preventive actions and to time them accurately. Rabies vaccinations seem to be the most effective way to control rabies epizootics (e.g. Aubert 1999). Bait-uptake would be maximised by placing the baits in the preferred habitats (Saunders *et al.* 1997). Culling (hunting) of animals might result in some unwanted effects, such as increased movements or increased breeding effort in the form of larger litter sizes (Frank & Woodroffe 2001) and even the "vacuum effect" (Bacon 1985), i.e. attracting new individuals to the emptied territories from the surrounding areas.

1.5. Aim of thesis

The aim of my thesis was to study the ecology of raccoon dogs, European badgers, red foxes and domestic cats and to discover how these species interact in a carnivore community. I interpreted the results in the light of disease (rabies) transmission and management. First, I reviewed the current knowledge of the ecology of rabies and the two main vector species, the red fox and the raccoon dog (I). Second, I studied the home range sizes and overlap and the dispersal distances of all four members of the carnivore community: the raccoon dog, the badger, the fox and the domestic cat (II). Third, I extended the view to the spatial and temporal interactions of these species (III). Last, I focused on how each species use their environment, i.e. the different habitats available and whether certain risky habitats could be identified in terms of the most used habitats and common habitats to all species (IV). In conclusions, I aimed to identify the essential species interactions in terms of rabies management.

2 Material and methods

2.1. Study area

The study area (land area 110 km^2) was located in the boreal zone, in Virolahti, southeast Finland about 9 km from the Russian border (60°32'N, 27°41'E; Fig 1). The area is a mosaic of agricultural land and commercial forests: coniferous (spruce *Picea abies*, pine *Pinus sylvestris*), deciduous (silver birch *Betula pendula*, downy birch *Betula pubescens*, black alder *Alnus glutinosa*, grey alder *Alnus incana*, aspen *Populus tremula*, bird cherry *Prunus padus*, rowan *Sorbus aucuparia*) and mixed forests. Large ditches run through the fields. Also, stone mines and seashore with large reed beds are special features of the area. A small village lies in the middle of the area. The mean temperature of the year during the study was 4.8° C, the mean being -6.3° C in January and 18.8° C in July. The ground was covered in snow from November or December until mid-April.

Raccoon dogs, badgers and foxes were regularly hunted in the study area. The main causes for the mortality of raccoon dogs and foxes were hunting, sarcoptic mange and lynx predation. None of the badgers died during the study.

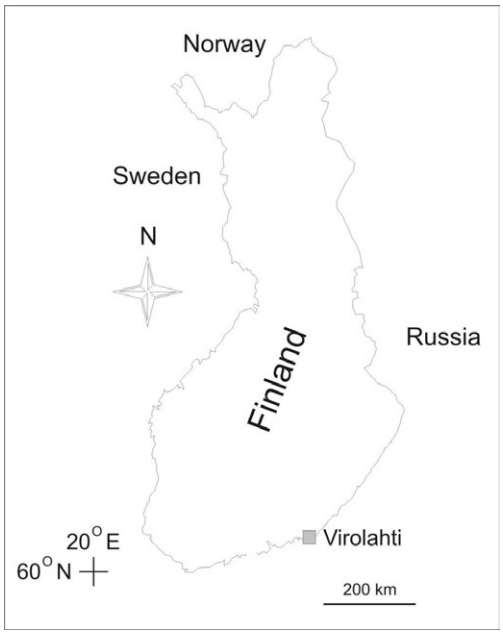


Figure 1 *The location of the study area in Finland.*

2.2. Trapping and radio telemetry

We captured the animals mainly by using wired or wooden baited traps. The animals were anaesthetized, except raccoon dogs, with an intra-muscular injection of ketamine hydrochloride. The animals were weighed, sexed and fitted with radio-collars (model TW-3, 138-138.5 MHz, Biotrack, Dorset, UK; and Televilt, Sweden) and plastic ear-tags (sheep tags, Dalton, UK). Transmitter life was about one year. Only adults were fitted with radio-collars.

We located the animals with a Yagi-type antenna once every 15 minutes during the dark hours. When possible, two

animals with overlapping home ranges were located simultaneously by two persons. Bearings were taken from at least two points, the time interval between the bearings being as short as possible, usually about 5 minutes, to minimize the error caused by animal movements. If the angle between the bearings were not close to 90°, we took a third bearing to make the location more accurate. The mean length of the tracking sessions was 5.0 hr ± 1.19 (Kauhala & Holmala 2006). Location error had been tested earlier, and was found to be < 150 m in 77% of the cases (Kauhala & Tiilikainen 2002). The mean distance between the tracker and the animal was 563 m (290-910 m) in a random sample of 30 locations (Kauhala *et al.* 2006). We gained data for 21 raccoon dogs, 6 red foxes, 8 badgers and 13 cats between autumn 2000 and summer 2004. The total number of locations was > 9 000.

2.3. Home range calculations

We calculated home ranges with the fixed density Kernel method (Kernel 95% or K95; Worton 1989, Kernohan *et al.* 2001) by using the reference smoothing parameter (1.0) with the software RANGES V and 6 (Kenward & Hodder 1996, Kenward *et al.* 2003) (Box 1). Species-specific core areas were defined from the utilization distribution curves (e.g. Jennrich & Turner 1969, Kauhala *et al.* 1993). Individuals were the sample units (Kenward 1992). The number of locations needed was tested for each animal (e.g. Odum & Kuenzler 1955, Kauhala *et al.* 1993).

2.4. Measuring interactions

Spatial analyses measure the spatial interactions of animals throughout a given time interval (Kernohan *et al.* 2001). The percentage of home range overlap (P_{area}) was calculated using the software Ranges 6 (Kenward *et al.* 2003). We also calculated the proportion of the animal's locations (%) in the shared area (P_{fix}). The ratio P_{fix}/P_{area} indicates spatial attraction to or avoidance of the shared area.

Temporal interaction analyses evaluate the relationship between animals at a particular point in time, which requires simultaneous locations for each pair of animals (Minta 1992). First, we calculated distances between simultaneous locations for each pair of animals. Next, we calculated Jacob's index of avoidance or cohesion to see whether the animals avoided, ignored or were attracted by one another (Jacobs 1974, Brown *et al.* 2000, Kenward *et al.* 2003). We also assumed that two animals were likely to come into contact during a tracking session, if > 10% of the same-time locations were within 100 m or > 20% were within 200 m or > 30% were within 300 m from each other. We also analysed the nightly routes of each pair of animals using the simultaneous locations, and counted the number of times their paths crossed.

Box 1 *Defining the animal´s home ranges.*

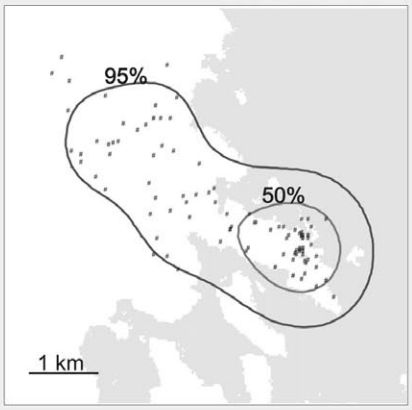
Box 1

The home range was first defined as " the area transversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt 1943). To get an objective estimation of this area, a statistical definition of the home range is used, in which a home range is defined by a utilization distribution (UD). UD describes the locations of an animal over time with a relative frequency distribution (Worton 1987, 1989). To exclude excursive activities, estimates of home ranges are often defined as the animal's locations 95% of the time (White & Garrott 1990; Fig. B1A).

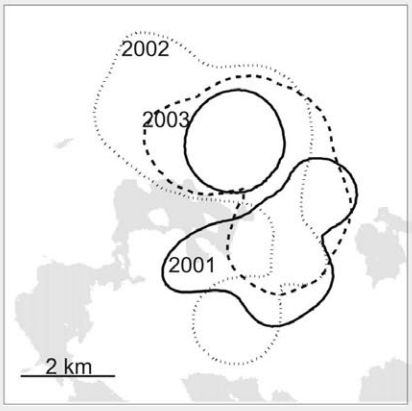
Kernel estimators have been suggested as more accurate means of estimating home range size (e.g. Worton 1987, 1989, Seamann *et al.* 1999) compared to some earlier methods, for example such as the harmonic mean method (Worton 1987, White & Garrott 1990) and the minimum convex polygon (Becoff & Mech 1984, Worton 1987).The kernel estimators are less sensitive to auto-correlation than the other home range estimators (Swihart & Slade 1997, de Solla *et al.* 1999), at least for species that exhibit unrestricted patterns of movement.

Although successive locations of each animal may not be independent, they can be used in home range calculations, if there are several tracking nights per home range (Smith *et al.* 1981) and the time interval between successive locations is relatively constant (De Solla *et al.* 1999). Voigt and Macdonald (1984) found that the nightly routes of adult foxes cover the whole home range in 1-5 nights. Furthermore, Rooney and his colleagues (1998) found that the correct strategy for the estimation of home range size would be the repeated use of as short a sampling interval as possible over an extended period of time. Since no locations in an animal's home range is completely independent from any other, one should not be overly concerned with eliminating auto-correlation from the data (Rooney *et al*. 1998, Baghli & Verhagen 2004).

In general, home range size depends on body mass and energy requirements, large species maintain large home ranges, and carnivorous species maintain larger home ranges than herbivorous species (Swihart *et al.* 1988). Habitat productivity may also influence home-range size (Swihart *et al.* 1988) and the home range boundaries may also shift between years (Fig. B1B).



B1A. Kernel 50% and 95% home ranges calculated for a fox. Gray area is water. Dots represent separate location points.



B1B. Home ranges (95%) of a female badger in three consecutive years.

2.5. Analysis of habitat selection and use

The habitat analyses were performed using Geographical Information Systems, mainly in ArcView and ArcGIS environments. Habitat selection was studied by comparing the habitat composition of the total home ranges to that of the study area. Habitat use within the home range can be described by comparing the habitat composition of the core area with that of the total home range (Porter & Church 1987). We defined two biological seasons: April-July ("summer", breeding and pup rearing) and August-October ("autumn", dispersal and preparing for the winter). The habitat use was characterized with a compositional analysis (Aebischer *et al.* 1993) and preference indices (Kenward 2001).

3 Main results and discussion

In the following, I discuss the results in the light of two main issues: (1) the interrelationships in the medium-sized carnivore community and (2) the implications of species behaviour for disease (rabies) transmission and management. The main study questions and the results are summarized in Table 2.

Table 2 *Main study questions and results.*

	Study questions	Main findings
I	What is known about the ecology of terrestrial wildlife rabies (excluding bats) and what are the characteristics of the main vector species, the red fox and the raccoon dog?	The number of rabies cases in wildlife has increased in recent years in Europe. The main vector species of rabies in Europe is the red fox. The importance of the raccoon dog has been increasing during the recent years, especially in the Baltic States. Important characteristics include animal density, home ranges and social organization, dispersal and winter dormancy.
II	What are the home range sizes of the raccoon dog, the red fox, the badger and the domestic cat? How much do home ranges overlap? What are the densities of these species?	Kernel 95% home ranges of badgers were the largest (mean 14.7 km^2) and those of the cats the smallest (1.5 km^2). Foxes had larger (6.6 km^2) home ranges than raccoon dogs (3.9 km^2). Home ranges overlapped largely between and within species, overlap being greatest between the home ranges of raccoon dog pair members and the least between neighbouring raccoon dogs. The density of adult raccoon dogs was the highest (7.7 ind./10 km^2), foxes 3.5 ind./10 km^2 and that of badgers` 2.6 ind./10 km^2.
III	What kind of spatial and temporal interactions do animals have? What is the risk of contact and contact rate between and within species?	Badgers, foxes and cats seemed to use the common area independently of conspecifics, whereas raccoon dog pair members favoured the common area. Raccoon dogs and badgers tended to favour their common area. Foxes favoured the common area they shared with raccoon dogs. The pairs of individuals whose nightly paths crossed most frequently were raccoon dog pair members, cats and raccoon dog–fox pairs. The risk of contact (certain part of simultaneous locations were less than 300 m apart) was highest for raccoon dog pair members and between cats and lowest between neighbouring raccoon dogs and neighbouring male foxes. The contact rate (the number of animals an individual might contact during a 3-day period) was highest for cats. Also raccoon dog-cat and raccoon dog–badger contact rates were high.
IV	Which habitats are selected from the landscape and which are used in the home ranges? Which habitats are included in the overlapping areas? Are favoured habitats risky habitats for rabies spread?	Raccoon dogs and badgers favoured especially deciduous forests and fields. Preferences of cats and foxes varied more, but for cats open areas and young mixed forests were important. The common parts of the overlapping home ranges of raccoon dogs and badgers included deciduous forests and fields, too. Therefore, deciduous forests, fields, young mixed forests and open areas could be identified as contact zones for different species and as risky habitats for rabies spread.

3.1. Intra-guild relationships of medium-sized carnivores

The home ranges of all four species overlapped considerably (Fig. 2); overlap was the highest between raccoon dogs and badgers (II). The badger home ranges were so large they covered large proportions of the home ranges of several other individuals of different species. Seasonal home ranges overlapped, too. Due to temporal overlap of home ranges individuals of different species moved frequently in each other's proximity (III). In general, the animals did not seem to prefer nor avoid each other's company. However, animals spent a lot of time near the borders of their home ranges and all species used the shared areas fairly often (III). Especially, raccoon dogs and badgers tended to favour the common area (III).

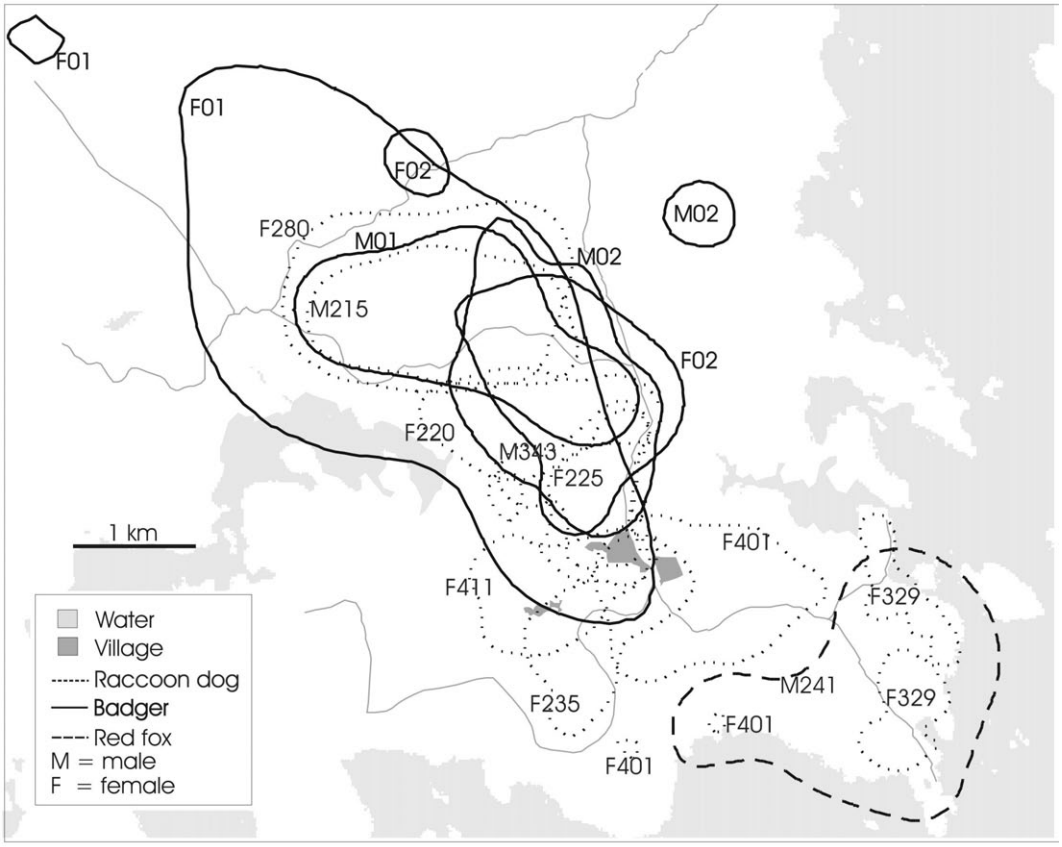


Figure 2 *Example of the overlapping total home ranges of raccoon dogs, badgers and red foxes from summer 2002.*

As calculated from the actual distances, contacts between individuals were very likely to occur during the nightly trips. Routes crossed (III), and commonly used paths could be easily seen among vegetation (own observation). For example, raccoon dogs had more contacts with individuals of other species than with conspecifics.

In this study, spatial partitioning of habitats between raccoon dogs and badgers was not evident during the summer and autumn as both species selected similar habitats (IV). The partitioning of the habitat use, i.e. spatial-temporal avoidance, could play an important role in the peaceful coexistence during times when habitat use overlaps highly. Furthermore, despite the co-occurrence of carnivores in some habitats, interfering carnivores may relax the effects of inter-specific competition either by temporal (Johnson *et al.* 1996) or spatial segregation (Rosenzweig 1966). All the species were equally active during the twilight hours. However, if raccoon dogs and badgers use the favoured habitats at different times of night, it may reduce the possibility of competition for the best food patches within the best habitats. Further research on the simultaneous habitat use is needed to test the presence of temporal habitat partitioning.

Raccoon dogs and badgers, and badgers and foxes are known sometimes to share dens (Kowalczyk *et al.* 2000, Kauhala *et al.* 2007, Kowalczyk *et al.* 2008, II). Moreover, in the study area, badgers and raccoon dogs changed their dens frequently, for example raccoon dogs changed their den 3 times during winter (Kauhala *et al.* 2007). Therefore, in winter, albeit that these species hibernate part of the coldest season, raccoon dogs and badgers might sometimes come into contact with each other.

Knowing how healthy animals use different habitats and contact other individuals makes it possible to estimate the contact rate between rabid and healthy animals. Both the frequency of encounters and contact rate of rabies vary between habitats (Macdonald & Bacon 1982). The nature of encounters is important for the spread of a disease. So far, there is no evidence of direct intra-guild aggression between red foxes and raccoon dogs. However, there are some observations about adult badgers killing raccoon dog pups, and adult raccoon dog killing badgers pups (Kowalczyk *et al.* 2008). The social system of each species greatly determines intra-specific interactions. Since the social system of badgers and red foxes varies between geographical areas, the knowledge of local circumstances is essential.

3.2. Interactions between conspecifics

The raccoon dog home ranges were a little bit smaller than in the previous studies in south-central Finland (Evo; Kauhala *et al.* 1993), but larger (Drygala *et al.* 2000), or about the same size as in Germany (Drygala *et al*. 2008b). The home ranges were largest in summer and the smallest in autumn (II). Food shortage in the early summer might be one reason for the larger home ranges. Raccoon dogs and badgers are known to reduce their movements before the onset

of winter dormancy in autumn (Kauhala *et al.* 2007). The raccoon dogs selected deciduous forests and fields to be included into their home ranges (IV). Within home ranges, they used more deciduous forests and fields in both seasons and more water edges in summer. In autumn, raccoon dogs also favoured mixed forests. Home ranges were larger in areas with a lot of coniferous forests indicating that the coniferous boreal forests are not the most optimal habitat for raccoon dogs. Habitat use differed from that of southern Germany (Drygala *et al.* 2008a) but results were similar to those from Ukraine and Russia (Nasimovic & Isakov 1985, Woloch & Rozenko 2007). The badger and raccoon dog home ranges sizes and the patch sizes correlated negatively, as did the home range sizes and the dispersion of the most favoured habitats (Holmala, unpubl.).

Raccoon dogs are monogamous (Kauhala *et al.* 1993, Kauhala & Helle 1994, Kauhala & Saeki 2004) without helpers, and the juveniles usually disperse from their natal area in autumn (Ward & Wurster-Hill 1990, Kauhala *et al.* 1993). Largely overlapping home ranges of the raccoon dog pair (II) confirmed that the pair is practically always together, which was also proved by the observed short distances between simultaneous locations (III). During their nightly search for food, the raccoon dog pair might come into contact with the neighbouring raccoon dogs. The home ranges of neighbouring raccoon dogs overlapped (II), but analysis of the use of the shared area and the simultaneous locations (III) further demonstrated that the animals ignored and sometimes avoided each other and therefore contacts would be relatively rare. The number of crossings between the nightly routes of neighbouring raccoon dogs was low, which also indicated a low frequency of contacts (III). Temporal avoidance might result in lesser intra-species competition in this area. In Mecklenburg, Germany, raccoon dogs showed a high tolerance towards conspecifics (Drygala *et al.* 2008b).

Within their Palaearctic distribution area, there is a great variation in spatial and social organization among different badger populations (Woodroffe & Macdonald 1993). Badgers in south-east Finland had larger home ranges than in most areas elsewhere in Europe (e.g. Rodriques *et al.* 1996, Br¢seth *et al.* 1997, Jedrzejewska & Jedrzejewski 1998, Kowalczyk *et al.* 2003). The home ranges were largest in spring, rather large still in summer and smallest in autumn (II). Home ranges of different individuals overlapped largely. Nevertheless, the social system of badgers was peculiar; badgers lived in low density with large overlapping home ranges but did not share a communal den (II). It is not known whether badgers in the area formed a social group (Cheeseman *et al.* 1987) or lived there independently from each other. The animals did not form lasting pairs (as in Poland; Kowalczyk *et al.* 2003) nor were they totally solitaire as in some areas (Johnson *et al.* 2002). However, two badgers would often rest in a same den both in summer and winter (II). In summer, they frequently changed their dens and companion.

The badgers selected deciduous forests and fields to be in their home ranges (IV). Within the home range, they used more fields and less other habitats in summer. In autumn, the badgers used more deciduous forests and field. The large home range sizes (II) and long travelling distances per night (Holmala, unpubl.) suggest that the heterogeneous boreal landscape offers relatively few good food patches for badgers.

The red foxes in the study area had rather large home ranges (II) as in Norway, Sweden and Poland (Lindström 1982, Overskaug *et al.* 1995, Goszczyński 1999). The home ranges of the foxes in the study area were larger than in most areas of continental Europe (e.g. Cavallini 1996, Baker & Harris 2004). The fox data were insufficient for assessing many parts of their behaviour. However, one male fox and two females shared their home ranges (II) and had frequent contact with each other (III). Individuals of the same sex tended to avoid each other (III). The foxes behaved as habitat generalists. Foxes had strong individual habitat preferences, and clear conclusions for the species are hard to make (IV).

The cats included in the present study were house pets and semi-feral cats. Home ranges of cats exhibit large variation depending on whether the cat is truly feral or semi-feral (e.g. Liberg 1984, Biro *et al.* 2004). The home ranges in the study area were about the same size in different seasons (II). The home ranges of the studied individuals overlapped. However, there were more cats living in the area than were included in the study. Thus, their true density would have bee even higher than the one recorded here. All the cats studied lived close to the village and farms and had frequent contact (III), and only few of them seemed to be more forest-oriented (IV). Most of the cats had owners and their home ranges were situated in the proximity of the owner's house. This area included more open area, field and deciduous forests than the landscape in general.

3.3. Implications of species behaviour for disease transmission and management

In addition to the fox, the raccoon dog has recently emerged as a second rabies vector species and is now thought to play a major role in the epidemiology and epizootiology of the disease in Eastern and Northern Europe (Botvinkin *et al.* 1981, I). Estimating the extent of disease transmission between and within species is a prerequisite to the effective control of undesirable diseases, such as rabies. There is evidence of substantial between-species transmission on diseases such as TB and rabies (e.g. Caley & Hone 2004). Therefore, decreasing the between-species transmission rather than within-species transmission may be a more efficient way to reduce disease spread.

3.3.1. Species behaviour and rabies transmission

The strong ecological links between the raccoon dog, the badger and the red fox provide the basis for the circulation of the virus between these species (I).

Because the home ranges of foxes, badgers and raccoon dogs overlap largely and their nightly routes often cross (II, III), they would probably also transmit the disease to each other. Also, in a case of rabies epizootic, members of a raccoon dog pair and members of the fox pair or family group would easily transmit the disease to each other, but it is also likely that they transmit the virus to neighbouring individuals of opposite sex. Therefore, intra-specific contact rates would be sufficient for rabies epizootic to persist, i.e. each individual transmits the disease to one or more individuals (I, III). Nevertheless, inter-specific interactions might be more important for disease transmission and during rabies epizootic (III, Fig. 3).

The raccoon dogs, the badgers and the cats selected deciduous forests and fields (IV). Therefore, the risky habitats or contact zones, i.e. habitats where species are likely to contact and transmit diseases to each other, could easily be identified. The same habitats were among the most used habitats within home ranges. Moreover, our analysis of the habitats in the temporally overlapping parts of home ranges demonstrated again the significance of deciduous forests and fields for raccoon dogs and badgers in both summer and autumn (IV). This also supports the interpretation that these common areas contain habitat patches that are preferred due to some valuable resources (i.e. food). These results further emphasise the conclusion that contacts between badgers and raccoon dogs could be even more likely than previously assumed, because both species favour the same habitats in the common areas.

Badgers and especially raccoon dogs occasionally visit yards and back gardens of houses. A few times also the foxes visited places with bird feeders near human settlement. There they are likely to come into contact with domestic cats and probably other free-ranging domestic animals. Because of the dense cat population, the contact rate between individual cats, and between cats and other species, is probably high (III). For example, cats frequently had contact with badgers and raccoon dogs and thus fell into danger of being infected and posing a threat to humans. The results show that deciduous forest patches and fields, too, are risky habitats in terms of contacts between domestic cats and wild medium-sized carnivores (IV).

The study showed a high level of overlap between home ranges both within and between species (II). It demonstrated that interspecies contacts (temporal overlap between individuals), were frequent, especially those between badger-badger and raccoon dog-badger pairs (III). The estimated contact rate (the number of possible contacts during the 3-night period) was so high (2.6–7.9) that a diseased individual would infect some individuals of the other species. Unfortunately, seasonal differences in the risk of contact could not be verified in this study.

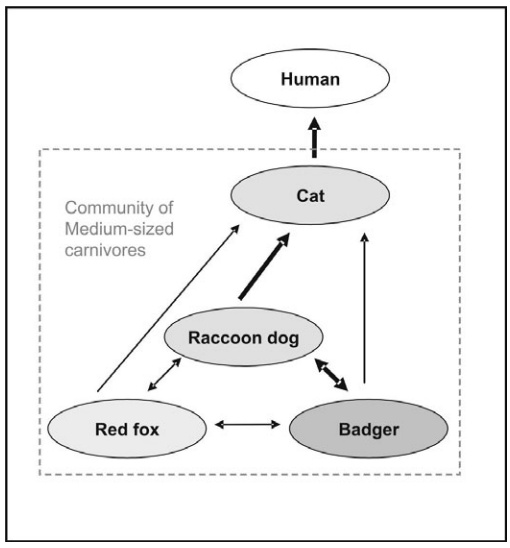


Figure 3 *The between-species transmission routes of rabies. Arrows in bold indicate the highest transmission likelihood based on contact rate analysis.*

Contacts are possible to occur also in shared dens. In the study area, some of the study animals had shared dens in winter (badgers and raccoon dogs)(II). Even though raccoon dogs and badgers hibernate part or most of the winter, they are also known to move around inside the den during this time. The observed encounters near feeding areas did not result in biting or other aggressive behaviour, but animals seemed to tolerate each other's presence (K. Holmala, own observation). So far, there is no evidence of direct intra-guild aggression between these medium-sized carnivore species in Finland.

3.3.2. Implications of the results for rabies management

Judging from the rabies case statistics, foxes and raccoon dogs are the main vector species in Europe (I). Badgers and cats represent the spillover species of sylvatic rabies. Due to the highest between species contact rates (III), vaccinations of raccoon dogs and badgers are the most effective way to reduce transmission rates between individuals susceptible to rabies infection. However, I do not recommend to stop vaccinating foxes but to reconsider the importance of badgers. To evaluate this, further information on bait-uptake by badgers and immunization rates may be necessary. Culling of animals might result in some unwanted effects, such as increased movement or increased breeding effort (Smith & Wilkinson 2003). Consequently, it would increase the between- and within- species contact rates. Furthermore, hunting of the immunized animals would be a waste of resources.

Oral delivery of rabies vaccines has proven to be the only effective rabies control method (Cliquet *et al.* 2008). In Finland, vaccinations are done twice a year to reach both the adult and the dispersing animals of both target species: red foxes and raccoon dogs (foxes dispersing usually in early springs, raccoon dogs in autumn). Bait-uptake would be maximised by placing vaccine baits in the preferred habitats (Saunders *et al.* 1997). In addition, placing of baits into these habitats might decrease the possibility of non-target animals consuming baits.

During the dispersal time in autumn, the most used habitats included field, deciduous forests and mixed forests (IV). Even the shared parts of overlapping home ranges of different species included deciduous forests more than

expected in random. Also, the densities of raccoon dogs, foxes and badgers were the highest in autumn. In the study area, the raccoon dog density in autumn was estimated to be 21 individuals/10 km^2, the fox density 6.5-8.1 foxes/10 km^2 and the minimum badger density 2.6 badgers/10 km^2 (II). High densities of animals result to more individuals susceptible for rabies. In areas of high densities of vector species, it is necessary to vaccinate a greater proportion of the population to eradicate a disease (Anderson & May 1985). This should also be taken into acount in the amount of vaccine baits delivered, especially in autumn. Otherwise, the result could be a lower immunization rate among target species (Artois *et al.* 1993, Cliquet *et al.* 2008). In the light of contact results, vaccination of badgers should also be considered.

The aspect of fox behaviour in the spread of rabies is widely acknowledged, although, many details are still poorly known (I). Due to the existence of two important vector species in eastern and northern Europe, multi-species rabies models are needed. Recent rabies models are development to include two vector species (fox-raccoon dog; Singer *et al.* 2008, 2009). However, in some areas there are more (and different) vector species involved in rabies epizootics (I). First results on multi-species models have shown that with two vectors of rabies the epizootic can occur at much lower densities of each species than was thought before (Singer *et al.* 2008). In addition, it seems that the density of raccoon dog alone is high enough to sustain an epizootic. Greater dispersal distances and larger territories at lower fox densities might also result in a higher rate of disease spread (Macdonald & Voigt 1985). Local rabies epizootic models taking into account the risky habitats could give us new insight on, for example, how the targeting of baiting could be further developed. Especially in urban areas, the density of housing could result in difficulties for baiting. However, urban green areas could be used as they are usually of the favoured habitat type (deciduous or mixed forests). Thus, applying habitat use information to risk assessment might help to make management decisions.

4. Conclusions

In this thesis I have studied how raccoon dogs, badgers, red foxes and domestic cats act as parts of carnivore community and how these interactions relate to the transmission risk of rabies. Since this study is so far the only published study where all four species have been radio-tracked simultaneously, we produced novel results on intra- and inter- specific interactions as well as species home range and habitat use.

These species form a community of medium-sized and rather generalist predators. They live in the same areas, in spatially and temporally overlapping home ranges and use the same habitats and dens and have similar diets. However, there is no direct evidence of competition. During this study, no aggressive behaviour towards other species was observed. Shared dens point to good tolerance of other species. Numerous observations of animals moving in each other's proximity give similar clues. The likelihood of competition is further decreased by the fact that, during summer, food is abundant, and during harsh winter, two of the species are asleep. In rural areas, the den sites are abundantly available, too.

These results have significant implications for disease management. In order to reach good management decisions, not only one or two species should be taken into consideration, but the whole community. In particular, this changes the perspective to animal densities, the densities of individuals susceptible to diseases and the magnitude of preventive actions. Rabies should be considered as multi-vector disease, at least in Finland and in Baltic states.

The topics addressed in this thesis are all essential components for building an explicit rabies model for Finland. It is of interest for the disease management to be able to model an epizootic with local parameters to reflect the real situation and also to suite best the local management needs. The current rabies models for Europe are based on fox ecology in western and central Europe. The next step from a one-species model is a multi-species model that includes relevant vector species. My results lead me to suggest that new models should be further developed with both foxes and raccoon dogs and even badgers as important vector species.

Acknowledging the afore-mentioned limitations of the data on foxes, the new insight of home range and habitat use gained by this study illustrates the similar favouring of certain, more productive, habitats by medium-sized carnivores thus creating a basis for contact zones, i.e. risky habitats for rabies transmission and spread. More effective vaccination bait uptake could be achieved if baits were spread out in these most used habitats, namely, deciduous forests and fields. Most likely, animals do not actively move in open fields but in fields and forests edges of and in the margins of ditches cutting the fields. In case of an epizootic, targeting the control measures to the most used habitats could result in a more cost-effective and rapid eradication of the disease. In Finland, the rabies

vaccination of pet cats is not regulated. However, the vaccinations of free-ranging cats, especially in rural areas, should be very strongly recommended.

We need still more research in order to really define the risky habitats for foxes and the social organization of badgers.

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